ECOLOGICAL, EVOLUTIONARY, AND CONSERVATION IMPLICATIONS OF FEEDING BIOLOGY IN OLD WORLD CAT SNAKES, GENUS *BOIGA* (COLUBRIDAE)

By

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ABSTRACT: Cat snakes forage actively and sometimes consume multiple prey items at a site. Some species use an unusual style of constriction and venom to immobilize prey, which is typically swallowed head-first. Approximately 300 prey items from 21 species demonstrate intra- and interindividual, ontogenetic, and geographic dietary variation. Most species of *Boiga* are small to moderately long snakes that eat mainly lizards, or large snakes that eat lizards as juveniles and mainly mammals and/or birds as adults. Probably predation on birds by introduced *B. irregularis* on Guam is a retained primitive feeding pattern, whereas that species' diet of rodents on New Guinea and euryphagy by *B. dendrophila* throughout its range are correlated with local ecological factors. With few exceptions (e.g., a mouse-deer in *B. dendrophila*), prey/predator mass ratios are not large compared to other snakes. Morphological and ecological considerations suggest that, like *B. irregularis,* several other species of cat snakes could have catastrophic impact as introduced predators on island bird and bat faunas.

INTRODUCTION

The Old World genus *Boiga* includes approximately 25 species of moderate to large, rear-fanged colubrids (Leviton 1970; Kroon 1973; Rasmussen 1979), often called cat or tree snakes because of their nocturnal, arboreal habits and vertical pupils. This report surveys published information on feeding in cat snakes, and analyzes additional data based on the examination of museum specimens. It addresses the nature of dietary and behavioral variation within and among 21 species of *Boiga,* and discusses ecological,

evolutionary, and conservation implications of that variation.

The feeding biology of cat snakes is of special interest for at least three reasons:

(1) *Boiga* is morphologically and ecologically diverse, and thus offers interesting material for broader evolutionary considerations. For example, although rear-fanged snakes play prominent roles in discussions of venom evolution (e.g., Smith and Bellairs 1947; Kardong 1979, 1980; Savitzky 1980), an understanding of that problem is hampered by a lack of information

on the feeding biology and phylogenetic relationships of informative taxa (Cadle 1983).

(2) Cat snakes might be important arboreal predators on vertebrates in many Old World tropical ecosystems, and three to five species of *Boiga* sometimes occur sympatrically (e.g., Taylor 1922a; Lim 1955; Lloyd et al. 1968; Kroon 1973; Inger and Colwell 1977). Autecological analyses provide data for subsequent community-level research, information that could not be obtained for snakes at a single site during a short-term study (Greene 1988a).

(3) Predation by *Boiga irregularis* was a key factor in the recent, precipitous decline of bird populations on the Pacific island of Guam, where that species was inadvertently introduced in the 1940s (Savidge 1984, 1987, 1988; Conry 1988; Fritts 1988). Island populations of fruit bats, already widely threatened by direct human persecution, might be at risk as well (Wiles 1988). Data on the natural diets of cat snakes could prove useful in managing this problem and preventing additional catastrophes.

METHODS

Stomach contents were examined through ventral slits in specimens in the Academy of Natural Sciences of Philadelphia (ANSP); American Museum of Natural History, New York (AMNH); California Academy of Sciences, San Francisco (CAS); Field Museum of Natural History, Chicago (FMNH); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Museum of Southwestern Biology, University of New Mexico, Albuquerque (MSB); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); and National Museum of Natural History, Washington (USNM). I avoided especially soft, brittle, or otherwise fragile specimens; all others for each species were examined to preclude a bias for large prey caused by opening only snakes with externally palpable food items. My results also incorporate data on 10 New Guinea specimens of *Boiga irregularis* that contained prey (R. Shine, in litt.) in the Australian Museum (AM) and Queensland Museum (QM), and specific published information on feeding. I took care to account for redundancy among literature records and museum specimens (e.g., Schmidt 1927 and Pope 1935; Smith 1916 and 1930), and sometimes obtained information not mentioned previously.

Direction of ingestion, identity, and linear dimensions of prey items were recorded whenever possible. Intact prey items (or a reference specimen of comparable size) and the predators were weighed after blotting and draining them briefly on paper towels. Abbreviations refer to snout–vent length (SVL), total length (TL), maximum total length (MTL), and prey/predator mass ratio (MR). All bird or lizard eggs in a stomach were counted as one item, because they might represent a single location event and because sometimes the exact number of items was impossible to determine.

SPECIES ACCOUNTS

Boiga angulata (Peters 1861)

Philippine Islands, MTL 1.4 m (Leviton 1970). Four snakes contained five agamid lizards (1 *Calotes* sp., 3 *Draco* sp., $\bar{x} = 1.3$/snake; Griffin 1910; CAS 154175, CAS-SU 24179; FMNH 61620). MRs for two *Draco* sp. in snakes with SVLs of 646 and 1,079 mm were 0.39 and 0.12, respectively. Two *Draco* sp. and an unidentified agamid were swallowed head-first.

Boiga blandingi (Hallowell 1857), Blanding's Tree Snake

Africa, MTL 2.7 m (Pitman 1974; Goodman 1985). Fifteen specimens contained at least 30 prey items ($\bar{x} = 2.0$/snake): a 1.8 m TL snake contained 1 agamid lizard (*Agama agama*) and ca. 8 bats (*Eptesicus tenuipennis*, Vespertilionidae; *Tadarida* sp., Molossidae); 5 each contained 1 bat; 1 contained bats and 1 lizard; 1 contained a chameleonid lizard; 1 contained 4 birds; 1 contained a sunbird (*Nectarina famosa*); 4 each contained 1 bird, 2 swallowed head-first; and 1 contained 3 bats, swallowed tail-first, MRs = 0.03/ each (Laurent 1956; Woodward 1960; Barry 1961; Cozens 1961; Dunger 1961; Menzies 1961; Pitman 1962; Hedges 1983; FMNH 179319–20; MCZ 54007). Three adults in one tree each contained young weaver birds, *Plesiositagra cucullatus*, and others contained fledgling birds and immature rats (Jones 1961).

Boiga ceylonensis (Günther 1858), Sri Lankan Cat Snake

India and Sri Lanka, MTL 1.6 m (Smith 1943). Forty-two prey items included 8 frogs (1 *Rana*

limnocharis, Ranidae; 5 *Philautus* sp., Rhacophoridae), 21 lizards (1 Gekkonidae; 2 *Calotes* sp., 3 *C. versicolor,* 1 *Charasia dorsalis,* 3 *Salea horsfieldi,* Agamidae), 3 birds (1 fledgling), and 2 mice (Wall 1919 [including snakes referred to as *B. nuchalis*], 1923, 1924; Hutton 1949; Taylor 1953; FMNH 131380, 167006). Two lizards were swallowed head-first.

Boiga cyanea (Dumeril and Bibron 1854), Green Cat Snake

India and Southeast Asia, MTL 2.3 m (Smith 1943). Seven snakes contained 1 snake (a female *B. cyanea,* 1,350 mm TL, in a 1,260 mm TL male) and 6 birds (1 sparrow [*Passer* sp., Passeridae], 1 probable wagtail [*Motacilla* sp., Motacillidae, in a snake of 821 mm SVL], 1 week-old domestic chick [*Gallus gallus,* Phasianidae]; Smith and Kloss 1915; Saint Girons 1972; Frith 1977; MCZ 58260). One bird had been swallowed head-first.

Boiga cynodon (Boie 1827), Dog-toothed Cat Snake

Southeast Asia and Indo-Australian Archipelago; MTL 2.8 m (Smith 1943; Saint Girons 1972; Kroon 1973; Tweedie 1983; FMNH 131809). Nineteen snakes contained 20 items ($\bar{x} = 1.05$/snake), including 3 lizards (*Draco* sp., *D. volans,* Agamidae; *Gekko gecko,* Gekkonidae), 12 birds, 4 or more bird eggs, and 1 rodent (Flower 1899; Auffenberg 1980; ANSP 26421; CAS 8533, 125173; FMNH 53454–6, 71628, 131809, 131811, 150883, 158652–3, 168006, 183749). One lizard, 1 rodent, and 5 birds were swallowed head-first. A small snake (SVL = 360 mm) had eaten a *Draco* sp., and a juvenile (SVL = 640 mm) contained a relatively large bird (MR = 0.44). An intact bird's egg, maximum diameter 51 mm, was swallowed by a snake with head length of 52.2 mm.

Boiga dendrophila (Boie 1827), Mangrove Snake

Southeast Asia and nearby archipelagos, MTL 2.8 m (Burger 1975; Tweedie 1983). Fifty-four prey items in 52 snakes ($\bar{x} = 1.04$/snake) included 1 frog, 15 lizards (9 scincids [2 *Lamprolepis smaragdinum*]; 2 lacertids, *Tachydromus sexlineatus;* 3 agamids [2 *Calotes* sp., 1 *C. cristatelus*];

1 varanid, *Varanus salvator*); 7 snakes (1 *B. cynodon,* 2 *Chrysopelea ornata,* 1 *Psammodynastes pulverulentus,* Colubridae; 1 *Calloselasma rhodostoma,* Viperidae); 17 mammals (2 bats [1 *Eonycteris spelea,* Pteropodidae], 1 mouse-deer [*Tragulus javanicus,* Tragulidae], 14 rodents [probably mostly Muridae, including *Rattus* sp.]); and 13 birds (Flower 1899; Smith 1916, 1930; Taylor 1922b; Brongersma 1934; Harrison 1962; Leviton 1970; Lim 1973; Minton and Dunson 1978; Smith 1985; ANSP 26417–8; CAS 12362–3, 15313; CAS-SU 28525–6; FMNH 53460, 53462, 53466, 68912, 71630, 96609, 120393, 131808, 150879, 158679, 178602, 230061).

Juvenile *Boiga dendrophila* eat mainly ectotherms (lizards and rarely snakes), whereas adults eat mainly birds and/or mammals (5/6 times vs. 25/34 items, respectively, using Brongersma's [1934] sample and museum records; $P = 0.01$, Fisher Exact Test). Sample sizes are insufficient for statistical comparisons, but I detect no evidence for major geographic variation in the diet of adults: frequencies of lizards, snakes, birds, and mammals, respectively, are 1, 1, 5, and 3 for Borneo; 5, 2, 2, and 5 for the Philippine Islands (all of the mammals were in Palawan mangrove snakes); 2, 1, 3, and 0 for Sulawesi; and 1, 3, 0, and 2 for mainland Asia. The largest snake containing a lizard and the smallest containing an endotherm had SVLs of 1,112 mm and 840 mm, respectively. Four lizards, 3 snakes, 3 birds, 4 rodents, and 1 adult mouse-deer were swallowed head-first, the latter by a 1.7 m TL snake. MRs for 2 lizards and a bird were 0.10–0.18 ($\bar{x} = 0.14$).

Boiga dightoni (Boulenger 1894)

India, MTL 1.3 m (Smith 1943). One adult (SVL = 915 mm) contained an agamid lizard, *Calotes versicolor,* swallowed head-first, MR = 0.24 (FMNH 217699 [Inger et al. 1984]).

Boiga drapiezii (Boie 1827), White-spotted Cat Snake

Southeast Asia, MTL 2.1 m (Tweedie 1954, 1983). Eight prey items included 5 lizards (1 Gekkonidae; 1 *Draco* sp., 1 *Gonocephalus* sp., Agamidae), 1 rhacophorid frog, and 2 birds (Lim 1956; FMNH 131804, 138594, 196805–6). Both agamids and the frog were swallowed head-first. MRs for the gecko and *Draco* were both 0.25.

Boiga forsteni (Dumeril and Bibron 1854)

Sri Lanka and India, MTL 2.3 m (de Silva 1980). Stomachs contained birds and a bat (Wall 1921).

Boiga gokool (Gray 1834),
Eastern Gamma Cat Snake

Asia and India, MTL 1.2 m (Smith 1943). Two snakes contained a mouse and an agamid lizard, the latter swallowed head-first (Wall 1910; MCZ 58261).

Boiga irregularis (Merrem 1790),
Brown Tree Snake

New Guinea, northern Australia, and nearby archipelagos; MTL 2.3 m (Fritts 1988). Fifty-nine snakes contained 65 items (1–3 per stomach, $\bar{x}$ = 1.10), including 2 frogs (1 *Rana* sp., Ranidae), 19 lizards (1 agamid, *Gonocephalus modestus*; 10 scincids [2 *Emoia cyanura*, 3 *Lamprolepis smaragdinum*], 8 gekkonids [1 *Gehyra* sp., 2 *G. mutilata*, 1 *Gekko vittatus*]), 13 birds (1 passerine, 1 owlet-nightjar [*Aegotheles bennettii*, Aegothelidae], 2 starlings [*Aplonis* sp., Sturnidae], 1 quail [*Coturnix chinensis*, Phasianidae]), and 30 mammals (1 marsupial bandicoot, Peramelidae; 1 bat; 1 shrew, *Crocidura* sp.; 17 rodents (5 juveniles, 1 adult *Rattus exulans*, 1 *R. rattus*, 1 *Mus musculus*, all murids; Rooij 1917; Kopstein 1926; Hediger 1933; Pendleton 1947; McDowell 1984; AM 4553, 11825, 12443, 12542, 14858, 86923, 87463, 87466; AMNH 40233, 42339, 42371, 59083, 62031–2, 65513, 73962, 85727–8, 85731, 95553, 95607, 101080, 101083; CAS 49910, 94027, 103388, 113600, 121224; FMNH 14076, 41980; QM 4381, 13.1280; USNM 6197, 61918, 61920, 159971, 195594, 213431, 215938, 215942, 215947, 216007, 216009, 237136, 237634). Stomachs with multiple prey included 1 with 2 *E. cyanura*, 1 with 2 *G. mutilata*, 1 with 2 young *Aplonis* sp., and 1 with 3 nestling rodents (apparently a single species). Three "bird" records consisted of 1 egg, several eggs, and 1 bird plus 2–5 eggs.

Forty-eight measurable individuals containing prey had SVLs of 292–1,710 mm. A 285 mm SVL specimen had an obvious umbilical scar, and six females containing enlarged ova or shelled oviductal eggs had SVLs of 840–1,305 mm. On those bases, I divided snakes containing prey into "juveniles" (equal to or less than 750 mm SVL) and "adults" (greater than 750 mm SVL). Juveniles take significantly more ectothermic prey (snake, frogs, lizards) vs. endothermic prey (birds, mammals), whereas adults show the opposite bias (14:3 vs. 6:32, respectively; $P < 0.01$, χ^2 test). The largest snake containing a lizard was 1,000 mm SVL, the smallest containing an endotherm was 646 mm SVL, and the shift from emphasis on one prey type to the other occurs at ca. 800–900 mm SVL (Fig. 1). Larger snakes ate larger prey than did smaller snakes (Fig. 2). Prey/predator mass ratios ranged from 0.004–0.241 ($\bar{x}$ = 0.106, n = 13), and the largest item was a 32 g starling (*Aplonis* sp.) in a 152 g *Boiga irregularis* from the Bismark Archipelago.

The 65 prey items are from throughout the species' range except for Australia, where the diet of this species is under study by R. Shine. There is significant geographic variation in diet ($P < 0.01$, χ^2 test) if 38 records for endothermic prey are divided into those from mainland New Guinea vs. those from smaller islands (all others except Sulawesi, including the Solomon, Bismarck, and Molucca groups). Snakes from New Guinea ate mammals more frequently than they ate birds (19:3), in agreement with summaries of unspecified numbers of prey (Room 1974; Parker 1982) and general comments about diet on the tags of AMNH 74506 and 82334. The single diet record from Sulawesi, also a "large island," was of a mammal. Snakes from "smaller islands" consumed birds and their eggs more frequently than they ate mammals (10:6).

Direction of ingestion was determined for 36 prey items. Twenty-eight were swallowed head-first, including 2 frogs, 8 lizards, 11 birds, 1 bat, 1 snake, and 5 rodents. Seven were swallowed tail-first, including 2 lizards, 1 bird, and 4 rodents. One lizard was swallowed bent doubled.

Savidge (1988) analyzed 494 prey items in 353 *Boiga irregularis* from an introduced population on Guam. As in natural populations, those snakes ate primarily lizards as juveniles and birds and/or mammals as adults. Her mean of 1.4 items/snake is higher than I observed, perhaps because she counted eggs as individual items in a stomach. Wiles (1988) reported three juvenile fruit bats in the stomach of a 2.5 m TL snake on Guam, and indirect evidence that these snakes were raiding bat roosts.

Boiga jaspidea (Dumeril and Bibron 1854),
Jasper Cat Snake

Southeast Asia, MTL 1.5 m (Taylor 1965; Tweedie 1983). Stomachs contained 1 agamid lizard (*Calotes* sp.), 1 bird, and 1 tree-mouse (*Chiropodomys gliroides*, Muridae) in a 1,213 mm TL snake (Lim 1956, 1967).

Boiga kraepelini Stejneger (1902)

East Asia and nearby islands, MTL 1.6 m (Kuntz 1963). Four snakes contained 2 agamid lizards (swallowed head-first), 2 birds, and 2 bird eggs, ready to hatch (Pope 1935; CAS 18891–2; FMNH 24986).

Boiga multifasciata (Blyth 1860),
Himalayan Cat Snake

Himalayan region, MTL 1.06 m (Smith 1943). One contained an agamid lizard, *Japalura variegata* (Wall 1909).

Boiga multomaculata (Boie 1827),
Large-spotted Cat Snake

East Asia, Java, Sumatra, and Borneo; MTL 1.2 m (Smith 1943). Stomachs contained 6 birds (1 *Motacilla* sp., Motacillidae) and 8 agamid lizards (*Calotes* sp., *C. versicolor*); three lizards (1 with MR = 0.58) and a bird were swallowed head-first (Wall 1926a, b; Schmidt 1927; Pope 1935; FMNH 26451, 105704, 178666; MSB 40769).

Boiga nigriceps (Günther 1863),
Dark-headed Cat Snake

South Asia and nearby archipelagos; MTL 1.7 m (Rooij 1917). One snake contained a bird, swallowed head-first (FMNH 128150).

Boiga ocellata Kroon (1973)

South Asia; MTL 1.7 m (Kroon 1973). Two adults contained a bird and a bird egg (FMNH 191998–9).

Boiga ochracea (Günther 1868),
Tawny Cat Snake

Asia, MTL 1.3 m (Smith 1943). Ten prey items included 8 agamid lizards (2 *Japalura variegata*,

3 *Calotes* sp.), 1 fledgling bird, and 1 mass of bird eggs; three of the agamids were swallowed head-first (Wall 1909, 1926a, as *B. hexagonatus*; CAS 12365, 95252).

Boiga pulverulenta (Fischer 1856),
Powdered Tree Snake

Africa, MTL 1.3 m (Pitman 1974). Ten snakes contained 13 prey items ($\bar{x} = 1.3$/snake): 3 mice (2 juvenile *Praomys* sp., Muridae, in 1 snake), 2 agamid lizards, and 8 birds (Werner 1909; Pitman 1974; FMNH 4017, 59006–7; LACM 38688, 46328; MCZ 29354, 29357; USNM 223775). Two lizards and 6 birds were swallowed head-first; 2 snakes containing lizards were 330 and 850 mm SVL, whereas 5 containing birds were ca. 700–780 mm SVL. MRs were 0.12 for each lizard and 0.15 for each of 4 birds in 2 snakes ($\bar{x} = 1.4$). One record of a bat in this species (Woodward 1960) is based on a misidentified *B. blandingi* (see above).

Boiga schultzei Taylor (1923)

Philippine Islands; MTL 1.4 m (Taylor 1923). A juvenile, SVL 310 mm, had swallowed 2 gekkonid lizards, *Gehyra mutilata*, head first (CAS 62153).

Boiga trigonata (Schneider *in* Bechstein 1802),
Gamma Cat Snake

Southern Asia, India, Sri Lanka; MTL 1.2 m (Smith 1943). ". . . the commonest contents were birds, chickens and eggs" (Lindberg 1932). Fourteen snakes contained 15 prey ($\bar{x} = 1.07$ items/snake), including 11 lizards (*Acanthodactylus* sp., Lacertidae; at least 4 *Calotes* sp., 2 *C. versicolor*, Agamidae; 1 scincid; 1 set of 3 lizard eggs) and 3 birds (1 *Saxicoloides fulica*, Muscicapidae); two lizards and 1 bird were swallowed head-first (Wall 1907a, 1919, 1921; Minton 1966; Sharma and Vazirani 1977; CAS 13686; FMNH 131958, 166998, 171761). Ants and grasshoppers in the stomach of a small Indian specimen (Sundersingh 1960) were probably remnants from the stomach contents of a prey lizard.

DISCUSSION

INDIVIDUAL AND GEOGRAPHIC DIETARY VARIATION.—Intraspecific variation in snake diets can include intra- and interindividual, on-

togenetic, seasonal, and geographic components (Arnold 1977; Greene 1984; Seib 1985; Mushinsky 1987; Macias Garcia and Drummond 1988; Savidge 1988). At one extreme, *Thamnophis elegans* (Colubridae) shows extensive geographic variation, and litter mates have genetic predispositions for alternative prey types (Arnold 1977); conversely, the diet of *Micrurus fulvius* (Elapidae) varies only slightly at all sizes and throughout the year over a large geographic range (Greene 1984).

In studies of museum specimens, evidence for intraindividual dietary variation comes from multiple prey types in single stomachs, as in a *Boiga ceylonensis* that contained a bird and two mice, and two *B. blandingi* that each contained bats and a lizard. All such records for *B. angulata, B. cynodon, B. dendrophila, B. irregularis, B. kraepelini, B. ochracea, B. pulverulenta, B. schultzei,* and *B. trigonata* apparently are multiples of one prey species, as are several records for *B. blandingi.* Of 353 *B. irregularis* on Guam that contained prey, 67 had more than one item of the same "prey type" (e.g., lizards and/or lizard eggs, birds and/or bird eggs): 14 had lizards and birds or mammals, as expected for small adults; and only five (<6% of stomachs with multiple items) contained birds and/or their eggs and mammals (Savidge 1988). These data suggest that individual cat snakes rarely eat birds *and* mammals, at least within a short time period. Some species, however, often consume more than one of the same prey type (and even same prey species), and perhaps this is especially true for *B. blandingi.* Surely the clumped distribution of roosting bats and nestling birds facilitates multiple ingestion.

There is significant geographic dietary variation in *Boiga irregularis* within its natural range, and microgeographic variation in predation on rodents vs. birds in urban vs. forest habitats by introduced snakes on Guam (data from Savidge [1988, table 1], χ^2 test, $P < 0.01$). The data for other species of *Boiga* are inadequate to distinguish geographic from individual and ontogenetic variation.

Perhaps diet is plastic at some localities, or throughout all or part of the range of some species of *Boiga.* If so, interspecific and geographic patterns could result from individual responses to local prey characteristics and/or availability, rather than from dietary evolution. The infre-

quent occurrence of multiple prey types in individual stomachs of several species of *Boiga* is consistent with stable prey preferences, whereas there evidently has been a rapid local response by *B. irregularis* to shifting prey densities on Guam (Savidge 1988, and see above; Greenwell et al. [1984] described a possible example involving *Thamnophis sirtalis* and birds on an island, and Chiszar [1989] discussed the behavioral basis for prey switching in *B. irregularis*). Genetic differentiation and phenotypic plasticity are not mutually exclusive, in that response to local conditions could override genealogically constrained prey preferences, and a thorough assessment of these possibilities for cat snakes will require studies of the ontogeny and control of feeding behavior in several populations.

PREY/PREDATOR SIZE RELATIONSHIPS AND ONTOGENETIC VARIATION. — As in other snakes (Greene 1984; Seib 1984, 1985), larger individuals of *Boiga* eat larger prey, and also continue to eat relatively small prey (Fig. 2). Most MRs for eight species of *Boiga* are not especially large compared with those of other snakes (0.004–0.58, $\bar{x} = 0.16$, $n = 32$; cf. Voris and Moffett 1981; Greene 1983, 1984, 1989; Seib 1984, 1985; Jayne et al. 1988). However, a 1.7 m *B. dendrophila* would weigh no more than 1 kg (pers. obs.) and lesser mouse-deer weigh 0.7–2.0 kg (Lekagul and McNeely 1977), so the latter is a relatively large item. A bandicoot in *B. irregularis* and prey snakes longer than the *B. cyanea* and *B. dendrophila* that contained them (Smith and Kloss 1915; Smith 1916) likewise were surely relatively heavy; a captive *B. irregularis* consumed a domestic rodent with MR = 0.60 (Chiszar 1989). Records for *B. irregularis* and *B. pulverulenta* demonstrate that a cat snake can ingest at least a third of its mass if it eats more than one item in a nest or roost.

Data from its natural range and the introduced Guam population agree that *Boiga irregularis* changes from eating mainly lizards to eating mainly birds and/or mammals at a SVL of ca. 80–100 cm. Similar shifts evidently occur in *B. dendrophila* and *B. pulverulenta,* and seem likely for other large species of *Boiga* (Fig. 1). Perhaps that pattern reflects simply an ability of larger snakes to swallow larger prey, since slopes and intercepts for endothermic vs. ectothermic prey are similar (analysis of covariance for data in Fig. 2, $P > 0.05$). However, large snakes eat endo-
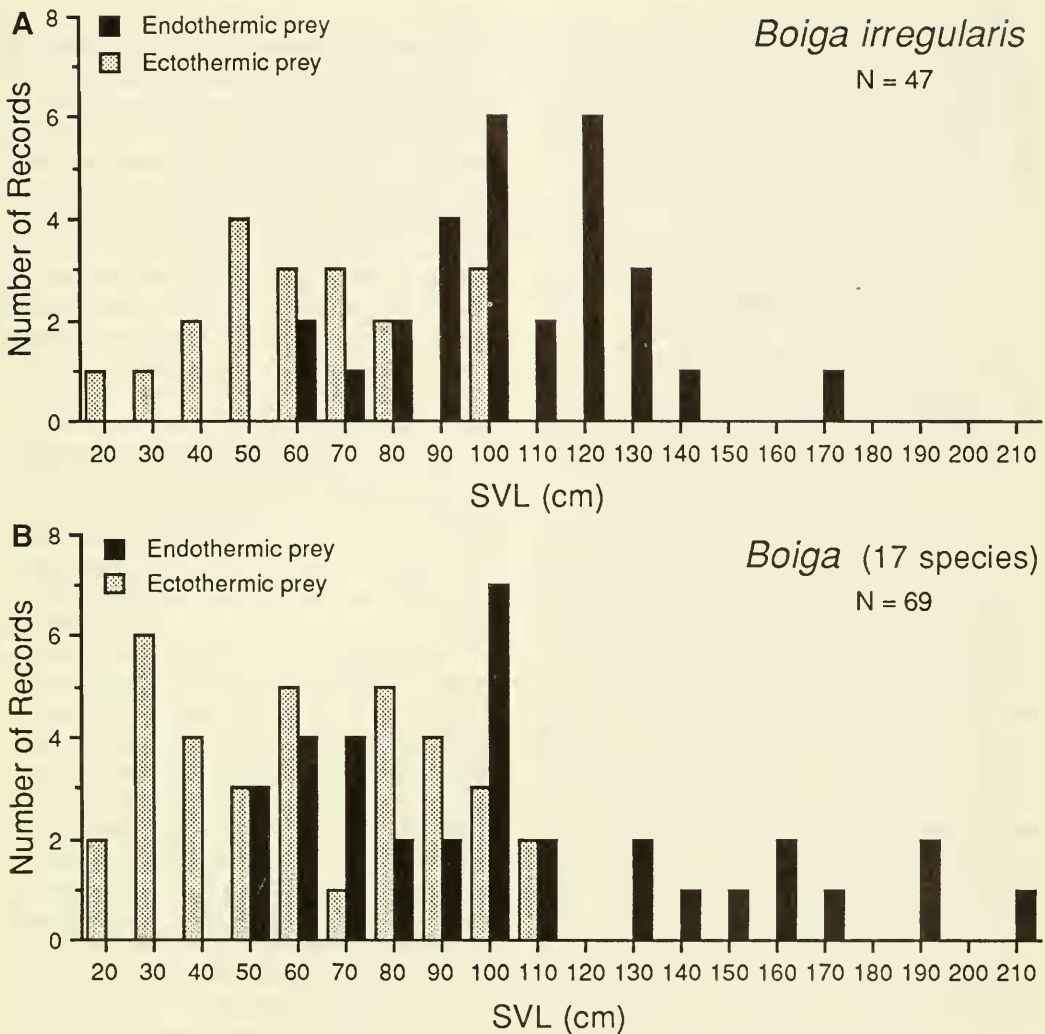
FIGURE 1.   Records for ectothermic and endothermic prey with respect to predator snout–vent length in cat snakes, genus *Boiga*. For this comparison, multiple items of one prey type in a single stomach were counted once.

therms that are smaller than the ectotherms taken by smaller snakes (Fig. 2), implying that larger snakes fail to encounter small ectotherms or have undergone a real change in prey preference.

FEEDING BEHAVIOR.—Most *Boiga* prey mainly on diurnal, arboreal lizards (especially agamids of the genus *Calotes*) and diurnal birds. Studies on free-living and captive *B. irregularis* suggest that these nocturnal hunters must search for rather than ambush inactive prey (Fritts et al. 1987; Savidge 1988; Chiszar 1989; Chiszar et al. 1985, 1988). Jones (*in* Pitman 1958) saw three *B. blan-*

dingi "pushing their heads into one nest after the other and taking the young [weaver birds]. . . ." However, a *B. dendrophila* constricting an *Eonycteris spelea* in a tree after dark probably ambushed the bat while it was feeding on or approaching fruit, as that species typically roosts in caves (Harrison 1962).

Some *Boiga cynodon, B. dendrophila,* and *B. trigonata* constrict prey with the tail as well as hold and presumably envenomate an animal with their teeth (Wall 1907b, 1921; Barach 1952; Murphy 1977; however, Lim et al. [1960] stated
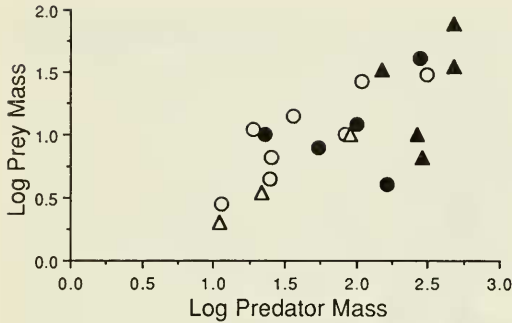
FIGURE 2.   Relationship between log predator mass and log prey mass for *Boiga irregularis* (triangles, *n* = 8) and eight other species of *Boiga* (circles, *n* = 13). Hollow symbols indicate ectothermic prey; solid symbols indicate endothermic prey. For this comparison, multiple items of one prey type in a single stomach were counted once.

that *B. cynodon* does not constrict prey). *Boiga multomaculata* constricts lizards, but the precise method is unknown (Campden-Main 1970). *Boiga blandingi* and *B. ceylonensis* do not constrict prey, whereas *B. forsteni* and *B. irregularis* vary in this regard (Groves 1973; Murphy 1977; de Silva 1980; Parker 1982; Shine and Schwaner 1985; Fritts 1988). Young (1983) observed that *B. blandingi* controlled prey with loops of the body, but did not constrict; that *B. cyanea* overpowered live mice with constriction "in a manner similar to that of a rat snake or a king snake"; that *B. cynodon* did not constrict, but controlled live prey with loose coils of the anterior body; and that *B. dendrophila* was "an efficient and powerful constrictor . . . upon warm blooded prey, but it rarely employed this behavior . . . on snakes." Captive *B. irregularis* swallow small prey immediately and apply constricting coils to relatively heavy prey (Chiszar 1989).

Additional inter- and intraspecific comparisons will be required to elucidate the variation in and evolution of prey-immobilization behavior in *Boiga.* Constriction with the tail is rare among snakes (Murphy 1977; Greene 1977) and absent in the outgroup to *Boiga* (see below), suggesting three possibilities: (1) It is a derived state for *Boiga,* either as yet unobserved or secondarily lost in most species; (2) some other derived attribute of *Boiga* (e.g., arboreality, long tails, multiple constriction of nestlings) favors this type of constriction and it arose repeatedly in the genus; or (3) constriction with the tail is a derived at-

tribute for a monophyletic subset of *Boiga,* a behavioral synapomorphy for those species.

The venom of *B. blandingi* is neurotoxic and can kill a large rodent or a small monkey in less than an hour (Wakeman 1966; Groves 1973; Levinson et al. 1976), and at least some other species have venom that is slightly or moderately toxic to humans (e.g., Deraniyagala 1955; Whitaker 1970; Burger 1975; Minton and Dunson 1978; Cox 1988; Fritts 1988). A captive adult *B. dendrophila* (TL ca. 1.8 m) had difficulty subduing and swallowing adult laboratory rats (Barach 1952), but those animals can be powerful opponents for captive snakes (pers. obs.).

Head-first prey ingestion is the norm in nature for *Boiga irregularis* (28/36 items, $P < 0.01$, χ^2 test), as it is for many other snakes (e.g., Greene 1976, 1983, 1984, 1989; Ananjeva and Orlov 1982; Voris and Voris 1983; Seib 1984, 1985). Of 61 cases for which direction of ingestion was determined for 16 other species of *Boiga,* 58 were swallowed head-first; 3 bats were eaten tail-first.

EVOLUTIONARY IMPLICATIONS.—An evolutionary consideration of feeding necessitates the categorization of dietary variation into alternative states and the identification of appropriate outgroups, so that the distribution of states among populations, taxa, and outgroups can be used to specify transformations during the history of that clade (see Arnold 1981; Kluge 1987; Losos and Greene 1988). A phylogenetic consideration of feeding in *Boiga* and its relatives, although based on incomplete data, has implications that justify the following preliminary analysis.

The precise relationships of *Boiga* to other colubrids are unknown; Rasmussen (1979, 1985) placed it with the African genera *Crotaphopeltis, Dipsadoboa,* and *Telescopus,* so these are used here as a collective outgroup. Species of *Crotaphopeltis* are terrestrial and feed on toads. Species of *Dipsadoboa* are arboreal and feed on frogs and lizards. The Eurasian species of *Telescopus* evidently are terrestrial, whereas the African *T. dhara* and *T. semiannulatus* are arboreal; all eat lizards and occasionally birds and bats. Species in all three genera are nocturnal and reach MTLs of ca. 1 m (Corkhill 1932; Pitman 1974; Broadley 1983).

Most species of *Boiga* are small to moderately long snakes that eat lizards throughout their lives, or large snakes that eat lizards as juveniles and endotherms as adults. Division of the second of

those qualitative groups into four subgroups yields a total of five dietary character states:

Diet-1 consists primarily of lizards throughout life, with an occasional bird or mammal. *Boiga ceylonensis* possesses this diet, as do perhaps *B. angulata, B. dightoni, B. gokool,* and *B. ocracea.* These species have MTLs of 1.2–1.6 m.

Diet-2 consists of lizards in juveniles, mainly of birds in adults. *Boiga cynodon,* some populations of *B. irregularis,* and *B. multomaculata* exhibit this diet, as do perhaps *B. drapiezii, B. forsteni, B. kraepeleni, B. nigriceps, B. ocellata,* and *B. trigonata.* These species have MTLs of 1.2–2.8 m.

Diet-3 consists of lizards in juveniles, mainly of rodents in adults. Only *Boiga irregularis* (MTL = 2.3 m) on New Guinea exhibits this state.

Diet-4 consists of lizards in juveniles, mainly of mammals and birds in adults. *Boiga blandingi* and perhaps *B. cyanea, B. jaspidea,* and *B. pulverulentus* exhibit this state, and have MTLs of 1.3–2.8 m. However, sample sizes are quite small except for the first species, and in no case can the possibility of geographic variation for diet-2 and diet-3 be excluded. Also, bats are probably functionally equivalent to birds in shape and arboreal roosting behavior (Cundall and Greene, unpubl.; many other snakes that eat bats also eat birds, Schaetti 1984), so that *B. blandingi* perhaps should be assigned diet-2.

Diet-5 consists of lizards in juveniles, mainly of snakes, birds, and mammals in adults. Stomach contents and observations on captives (Young 1983) suggest that *Boiga dendrophila* is more euryphagic than other species in the genus.

Ingroup and outgroup comparisons indicate that *Boiga* is primitively nocturnal and perhaps derivatively arboreal. Diet-1 and relatively small MTL are found in a few species and in the outgroup, but lacking knowledge of intrageneric relationships, we cannot determine if their presence in *Boiga* is primitive or a reversal. Diet-2 and large size are widespread in species of *Boiga* and absent in the outgroup (with the possible exception of diet-2 in some *Telescopus*), but we cannot be sure if those characteristics are derived for the genus or within *Boiga,* perhaps more than once.

Diet-2 is probably primitive for adult *Boiga irregularis,* based on widespread occurrence in the genus, suggesting that diet-3 is derived within that species, but the reasons for intraspecific geographic variation are not known. Birds are rarely eaten by *B. irregularis* in New Guinea, although the island has a rich avifauna (Beehler et al. 1986). Several species of New Guinea birds exhibit nesting attributes that are possibly antipredator specializations (J. M. Diamond, University of California, Los Angeles, in litt.), but perhaps so do birds on other islands and the mainland that are commonly eaten by other species of *Boiga.* A niche shift in response to competitive pressure seems unlikely, because no other New Guinea snakes are known to feed heavily on birds (McDowell 1969, 1972, 1975, 1984; Shine 1980a; Parker 1982; Malnate and Underwood 1988). Perhaps New Guinea arboreal rodents are so much more diverse and numerous than on nearby archipelagos (Laurie and Hill 1954; Menzies and Dennis 1979) that they provide "better" food per unit effort or are simply encountered more often than birds.

Based on ingroup and outgroup comparisons, diet-4 and diet-5 are probably derived within *Boiga.* Euryphagy evidently reaches a maximum for the genus in *B. dendrophila* and is correlated with a derived preference for riparian habitats (Taylor 1965; Frith 1977; Minton and Dunson 1978; Dring 1979; Cranbrook and Furtado 1988; this proclivity is not reported for other species of *Boiga* or the outgroup genera). Some theoretical foraging models predict that habitat specialization results in broader diets and use of suboptimal prey (e.g., MacArthur and Pianka 1966; Krebs et al. 1983). The relevance of those models for cat snakes could be explored with captive animals, in part, by testing the presumption that alternative prey types vary in profitability (see Godley 1980).

My findings on feeding biology in *Boiga* underscore some cautionary lessons with regard to the evolution of rear-fanged snakes:

(1) Ontogenetic and/or geographic variation can be sufficiently large that a proportional representation of overall diet for a species will obscure functional, biogeographic, and phylogenetic correlates: the overall sample for *Boiga irregularis* from throughout its natural range consists of approximately 32% lizards, 21% birds, and 44% mammals, but most individuals feed *entirely* on lizards as juveniles and on either mainly rodents *or* mainly birds as adults.

(2) The preceding analysis assumes that diets really are attributes of populations and taxa, and

that they have evolved conservatively (i.e., with minimal homoplasy). High rates of reversals and convergence can only be detected by detailed phylogenetic analysis, so there is as yet no basis for postulating this alternative for *Boiga*. The other possibility, that individual dietary plasticity accounts fully for geographic and systematic patterns, is discussed above (see INDIVIDUAL AND GEOGRAPHIC DIETARY VARIATION).

(3) There is no evidence that the venom apparatus of *Boiga* is functionally associated with feeding on prey that are especially heavy or otherwise costly, although rare ingestion of large prey remains a possibility (see *B. dendrophila,* above, and Greene 1986a).

(4) Rear fangs arose at the level of *Boiga* or, more likely, a more inclusive group (Rasmussen 1979, 1985). Whatever the ecological role of venom injection (if any) in extant cat snakes, its possible adaptive origin (if any) in the clade containing *Boiga* cannot be identified until additional information on suprageneric relationships and natural history are available (see Cadle 1983; Greene 1986a; Schaefer and Lauder 1986). To the extent those limitations apply to other clades, conclusions about the adaptive significance of rear-fanged dentition are premature.

ECOMORPHOLOGICAL SUITES AND CONVERGENT ANALOGUES. — Qualitative ecomorphological analogs have been identified among certain geographically and phylogenetically distant snakes (e.g., Shine 1980a, b, c; Henderson and Binder 1980), and suggestive parallels can be drawn between species of *Boiga* and certain other taxa. Some resemblance to Afro-Asian species of *Telescopus* might be either convergent or homologous (Rasmussen 1979, 1985); the two genera are largely allopatric. Rear-fanged colubrids of the Malagasy genus *Lycodryas* (Raxworthy 1988) and neotropical genus *Imantodes* (especially the *I. cenchoa* species group, Myers 1982) are arboreal, nocturnal, and resemble small species of *Boiga* in general body form (e.g., large head and eyes, slender neck) and diet. The New World, rear-fanged genus *Trimorphodon* is said to be related to *Boiga* (Dowling et al. 1983) or to several genera of New World colubrines (Minton and Salanitro 1972; Cadle 1988; R. Lawson, CAS, pers. comm.). Both species of *Trimorphodon* are arboreal, nocturnal, and feed largely on sleeping, diurnal iguanid lizards; only certain populations of *T. biscutatus* occasionally include birds and

bats in the diet (Greene, unpubl. data). A non-venomous, diurnal neotropical colubrid, *Pseustes poecilonotus,* resembles *B. dendrophila* in size, diet, and defensive behavior; however, even juvenile *P. poecilonotus* eat small birds (Greene 1979, and unpubl. data). I detect no particular convergent resemblance, beyond arboreality, irrascibility (Greene 1988b), and nocturnality, between *Boiga* and Australian elapids of the genus *Hoplocephalus* (Shine 1983).

CAT SNAKES AS INTRODUCED PREDATORS. — This study provides potentially useful insights with regard to the threat that introduced cat snakes pose for island prey faunas:

(1) Heavy predation on birds by *Boiga irregularis* on Guam probably reflects the primitive diet for this species (see above), rather than a feeding shift in response to special local conditions. It is not surprising that this snake makes heavy inroads on island bird populations, especially if acceptable alternative prey (e.g., rodents, see above) are unavailable or rare, and/or if the native avifauna has evolved behavioral and demographic attributes in the absence of predators (see Jackson [1974] for a bird with behavioral defenses against nest predation by snakes). The effects of an introduced snake on native island prey populations might be all the more rapid in the absence of natural predators on snakes (Greene 1988a).

(2) Neonate *Boiga irregularis* are evidently too small to eat endothermic prey, and starvation of juveniles is probably a major source of natural mortality in some snake populations (e.g., Fitch 1949). Potential control measures for introduced *Boiga* might include manipulating the availability or characteristics (e.g., artificial toxicity) of lizard prey.

(3) *Boiga irregularis* is a moderately large snake with a venom delivery system and constricting behavior that could permit it to subdue a wide range of prey sizes and types. Like several other species of *Boiga,* it possesses a relatively wide skull and long dentaries (Marx and Rabb 1972), derived characteristics that are likely associated with increased gape (Rasmussen 1979; Arnold 1983), thereby facilitating a diet of birds, eggs, and bats (Cundall and Greene, unpubl. data). Although not so highly specialized as to be unable to forage on the ground, evidently all species of *Boiga* climb well and are nocturnal.

Each of the above attributes of cat snakes might

enhance their ability to feed on sleeping diurnal birds and their eggs, or on roosting and foraging bats. For those reasons and/or because of known predation on birds and bats, all moderate to large *Boiga* are potentially catastrophic invaders of isolated island faunas. Species for special concern include *B. blandingi, B. cyanea, B. cynodon, B. dendrophila, B. drapeizii, B. forsteni, B. irregularis, B. jaspidea, B. kraepelini, B. nigriceps, B. ocellata, B. pulverulenta, B. schultzei,* and *B. trigonata.* There is a clear potential for additional introductions: recently individual *B. irregularis* have reached several Pacific islands (Fritts 1988), at least one *B. dendrophila* landed on Taiwan in a shipment of lumber (A. H. T. Yu, pers. comm.), and several species of large *Boiga* are commonly available in the pet trade (pers. obs.).

Epilogue

I have never seen a *Boiga* in the field, and this research was made possible by the efforts of numerous collectors, curators, authors of anecdotes, and sponsors of natural history publications. Few of those individuals intended their specimens for studies on the evolution of feeding, and even fewer imagined that their labors would have implications for an urgent conservation problem. Nevertheless, starting from scratch to learn something comparable about the broader context for avian predation by introduced cat snakes on Guam would have required many years of work. Therein surely lie some lessons (see also Greene 1986b; Greene and Losos 1988).

Acknowledgments

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